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Finally we may write

$$p = \int \frac{1}{\rho_0} \sqrt[3]{\frac{r_0}{2r}} ds, \quad (12)$$

where  $r$  has the same meaning as in (11), where  $\rho_0$  is the distance from the point  $P$  of the curve to the center  $M$  of the corresponding osculating conic, and where  $r_0$  is the radius of curvature at  $M$  of the locus which  $M$  describes when  $P$  moves along the given curve.

<sup>1</sup>E. J. Wilczynski, *Projective Differential Geometry of Curves and Ruled Surfaces*, p. 58.

<sup>2</sup>Loc. cit., p. 59.    <sup>3</sup>Loc. cit., p. 60.    <sup>4</sup>Loc. cit., pp. 67-68.

## SIZE INHERITANCE IN GUINEA-PIG CROSSES

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For several years my pupils and I have been engaged in studying the inheritance of size and weight differences among animals, these being characteristics of much economic importance and of peculiar theoretical interest. Preliminary studies published in 1909 showed that size and weight in rabbits do not follow the Mendelian rules of dominance and segregation as unit-characters. But Lang subsequently suggested that multiple Mendelian factors may be concerned in such cases, extending to animals a principle already recognized by Nilsson-Ehle in dealing with certain categories of characters in plants. Punnett and Bailey (1914) accept this principle in explaining weight inheritance in crosses of bantam fowls with those of ordinary size. They believe that four differential factors are concerned in a particular cross studied, three dominant factors which tend to increase size being found in the larger race, one such factor being found in the bantam race. By recombination in  $F_2$  some individuals are obtained smaller than the bantam race, and others in  $F_3$  larger than the larger race. But there are some reasons for questioning the validity of this analysis which assigns very definite quantitative values to the several hypothetical factors, without however making any allowance for physiological changes of size due to non-genetic causes, or for possible quantitative variation in the factors themselves. Moreover, let it be granted for the sake of argument that these four Mendelizing factors exist and that each is an independent agency for increasing size. On the Mendelian hypothesis there should be obtained from the cross in question individuals which lack *all four* of these factors. What, it may be asked, will their size be? Will they be with-

out size or devoid of genetic variation in size? No race of animals has yet been shown to exist which is devoid of genetic variation in size,—Jennings' supposed demonstration of such a condition in asexually reproducing *Paramecium* having been disproved by the work of Calkins and Gregory and his own subsequent work on *Diffugia*. If when all discoverable Mendelian factors are wanting size still varies genetically, a Mendelian explanation of size inheritance proves itself inadequate. There also exists a possibility that *bantamness* in fowls involves discontinuous variation such as does not occur in ordinary size differences. For Phillip's results with ducks do not show such segregation of the extremes of size as Punnett and Bailey record, though his crosses were made between races of ducks both very pure and very different from each other in average size. What Phillips observed was a blend with a slight increase of variability in  $F_2$  but without evidence of complete segregation or recombination of size factors.

Some excellent material for the study of size inheritance has become available to the writer in certain very pure races of guinea-pigs differing widely as to size and it is the purpose of this note to describe briefly the more important results obtained and their possible significance. Attention is invited to the nature of the growth curves observed for the races crossed and to non-genetic as well as to genetic factors affecting size.

Three distinct and unrelated races were used in the crosses to be described. First, a wild race obtained at Arequipa Peru in December 1911, and identified as *Cavia Cutleri* Bennet. This has been bred for three generations in captivity at the Bussey Institution and has shown itself very uniform in size and other characters. Second, a race of guinea-pigs which we may call race B, bred distinct for many years at the Bussey Institution, very uniform in size, and varying as regards Mendelian factors only in respect to the color factor. Some animals of this race are black, others are albino. Both sorts are alike as regards other characters. A race C, also long bred distinct at the Bussey Institution, is of about the same average size as race B. It as well as race B has been used in crosses with *C. Cutleri*, but the hybrids from these two crosses have not been interbred, though the data concerning them have been combined for statistical treatment.

Figure 1 shows separately growth curves for the two sexes of race B and *Cavia Cutleri*. These curves have been obtained by combining the individual growth curves of several different animals reared in captivity and weighed at intervals of one or two weeks. They represent *averages* and the curves have been smoothed somewhat. It will be observed that the young of *Cutleri* grow rapidly for the first 40 or 50 days of their

lives after which increase in weight slows up gradually and finally ceases altogether at the age of about one year. Both sexes are of about the same size at birth but females grow at first faster than males, attaining sexual maturity some weeks earlier. At about fifty days of age the sexes are again of the same average size, but from this time on the males are heavier. The general form of the growth curve in both sexes is, as in animals generally, at first concave upward but later becomes convex upward as the growth rate declines. Growth is completed at about one year, after which time no change in weight occurs except as caused by health or food conditions, or pregnancy of the females. The growth curve of *C. Cutleri* may be characterized as a sharply rising, flat curve. Compared with this the growth curve of the domesticated race B rises less rapidly at first but continues its rise longer. The same difference

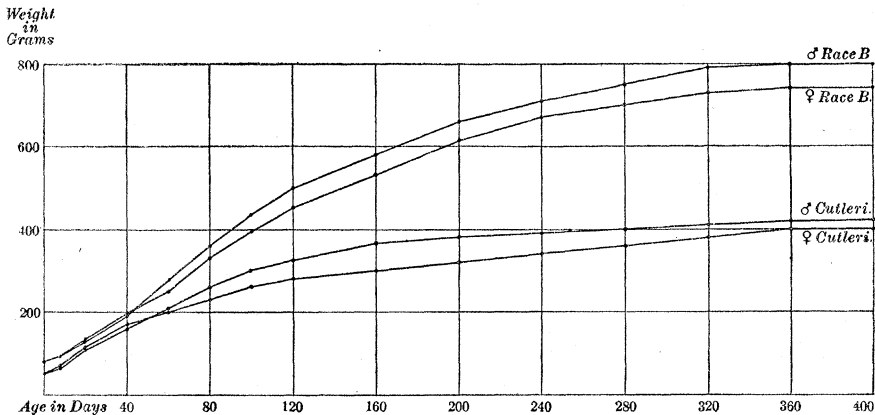


FIG. 1. GROWTH CURVES OF RACE B GUINEA-PIGS AND OF *CAVIA CUTLERI*.

in the growth rate of the sexes is observed in race B as in the wild *C. Cutleri*. Females grow faster up to 40 or 50 days of age, after which time males permanently take the lead. The adult weight of race B animals is approximately double that of *Cutleri* individuals.

In figure 2 are reproduced for comparison the growth curves of the females of both race B and *Cutleri* and along with these are plotted the growth curves of  $F_1$  and of  $F_2$  females produced by crossing *Cutleri* males with females of race B and race C. These curves show that  $F_1$  females are larger at birth than females of either parent race and that they remain continuously larger having at maturity a size slightly larger than that of either parent race. That this increased size is not due to heredity, but to a growth stimulus produced by the crossing of unrelated parent races, a 'law of hybridization' formulated by Focke (1881), is shown by

an examination of the  $F_2$  growth curve, which is everywhere lower than the  $F_1$  growth curve. The  $F_2$  females are indeed, like  $F_1$  females, at first larger than young of either pure race and continue this lead for three or four months, but from that time on their growth rate slows up notably and falls below that of race B so that at maturity they are nearly intermediate in size between the parent races. The  $F_2$  females, as a group, have a rapid early growth like that of the Cutleri parent but lack the staying qualities of race B as regards growth so that from an age of about 150 days on they fall below race B in size. Accordingly, though the growth curves of both parent races and of the  $F_1$  females are so far parallel in general course that they do not cross each other, the growth curve of the  $F_2$  females crosses and falls below that of race B attaining at length an intermediate position between Cutleri and race B. This, so far as heredity is concerned, we may assume to be its true position,

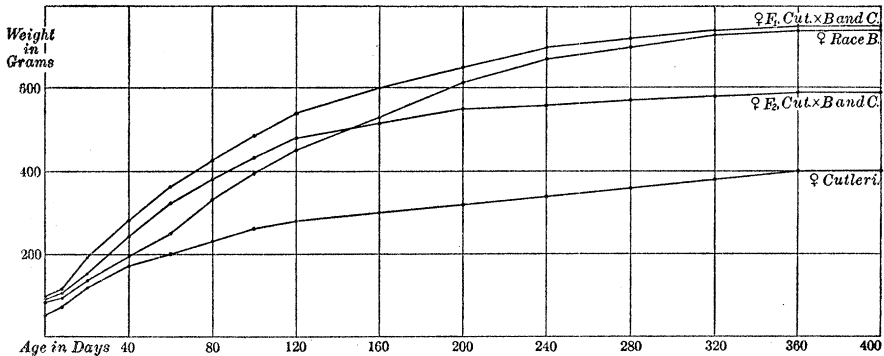


FIG. 2. GROWTH CURVES OF RACE B AND CUTLERI FEMALES AND OF THEIR FEMALE HYBRIDS BOTH  $F_1$  AND  $F_2$ .

the added size of  $F_1$  females being due not to heredity but to a growth impetus arising from hybridization, in accordance with Focke's law.

Figure 3 shows that the statements made concerning female hybrids are true also for male hybrids in crosses between Cutleri males and females of race B or race C. In this case the superior size of  $F_1$  hybrids, as compared with the parent races, is even more strongly in evidence, while  $F_2$  hybrids, though larger than either parent race for about four months, from that time on are of intermediate size. But for some reason, possibly not due to heredity, their ultimate size is nearer to that of race B than to that of the Cutleri parent.

It might be supposed that the size inheritance in crosses of a wild species with a domesticated race may be different from that in crosses between different domesticated races. To test this matter crosses were made between females of race B and a male guinea-pig obtained in the

cabin of a native in Arequipa, Peru, this Arequipa guinea-pig being of a size about one half greater than that of race B males. The growth curve of race B males is shown in figure 4 where it can be compared with the growth curves of  $F_1$  and  $F_2$  male animals obtained by crosses of the Arequipa male with race B females. It will be observed that the growth curve of the  $F_1$  males runs a course in general parallel with that of the growth curve for race B males but at a much higher level. The growth curve of the  $F_2$  males starts in at a still higher level, perhaps in part because the vigorous  $F_1$  mothers supply an abundance of nourishment to the young. But from weaning time on (age about 20–30 days) the  $F_2$  males grow less rapidly. Their curve crosses the  $F_1$  curve at 40 days and continues thence below it so that its ultimate position is

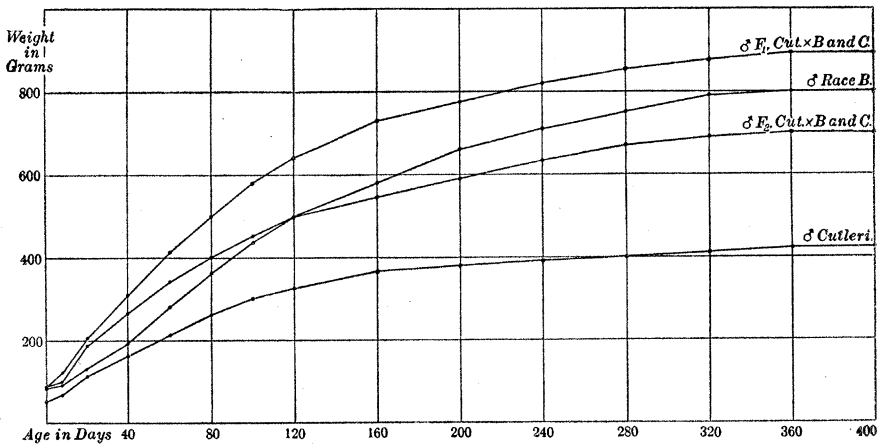


FIG. 3. GROWTH CURVES OF RACE B AND CUTLERI MALES AND OF THEIR MALE HYBRIDS BOTH  $F_1$  AND  $F_2$ .

intermediate between the  $F_1$  and the race B growth curves. It is evident that here, as in the Cutleri crosses, the  $F_1$  animals are larger than heredity alone would make them, that they have an added size due to a growth stimulus produced by hybridization, but that this added stimulus is largely dissipated in  $F_2$ , which accordingly shows blended or intermediate heredity. It is evident that Mendelian dominance is wanting in these size crosses. It remains to inquire whether segregation also is wanting. The individual growth curves of  $F_1$  and  $F_2$  animals give no very clear evidence on this point. Too many environmental factors enter into the problem, such as time of year, food conditions, accumulation of fat in old age, and the like, which, while they do not affect the *average* growth curves already discussed, do obscure the question of

segregation in individual cases. Bone measurements are believed to be less affected by extraneous influences than the growth curves of individuals. Consequently our inquiry as to evidences of segregation will be confined to them. Three different bone measurements have been studied for each full grown individual (age 13 months or over, in most cases). These are maximum skull-length, maximum skull-width, and femur length. The facts arrived at are contained in Tables 1-3.

In the first part of Table 1 is shown the variation in skull-length of 10 full grown Cutleri females and of 28 full grown race B females. Measurements were made with a caliper rule furnished with a vernier,

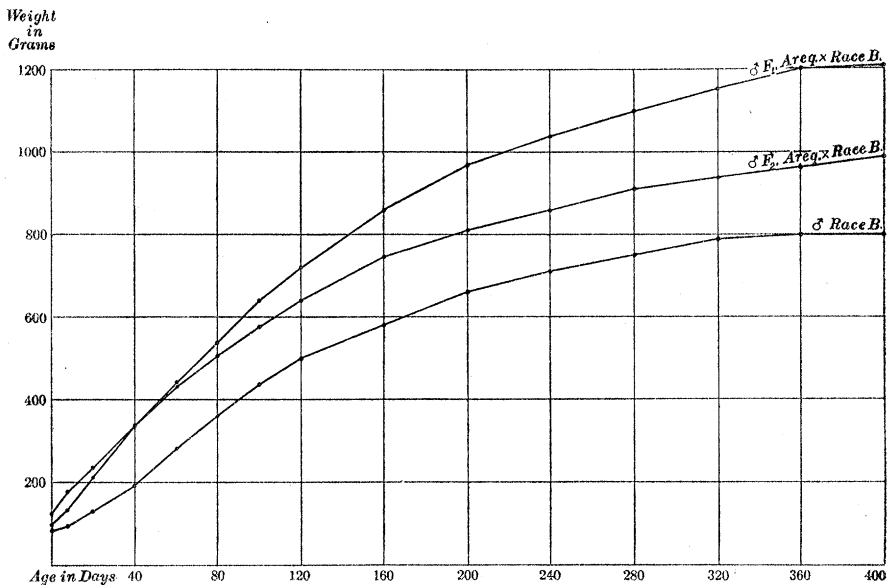


FIG. 4. GROWTH CURVES OF RACE B MALES AND OF THE MALE HYBRIDS BOTH  $F_1$  AND  $F_2$ , PRODUCED BY A CROSS WITH THE AREQUIPA RACE.

and are accurate within 0.1 mm., the possible observational error shown by repeated measurement. The measurements are classified in classes of 0.5 mm. range numbered in order of increasing size. The lowest class, that numbered 1, would include measurements 48.5-48.9 mm.; class 2 would include measurements 49.0-49.4, etc. The absolute measurements included within each class of the table may thus be readily calculated, if desired. They are omitted for simplicity. The Cutleri females measured range in skull-length from class 1 to class 10. The race B females range from class 11 to class 25. Thus the two races do not overlap in range. Race B begins where Cutleri leaves off. Their means are 6.6 mm. apart.

TABLE 1  
VARIATION IN SKULL-LENGTH OF CAVIA CUTLERI AND OF CERTAIN RACES OF GUINEA-PIGS AND OF THEIR HYBRIDS  
CLASS 1 INCLUDES MEASUREMENTS 48.5-48.9 MM.

0.5 MM. CLASSES																																						TOTALS	MEANS	$\sigma$																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																															
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																		
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TABLE 2  
VARIATION IN SKULL WIDTH OF CAVIA CUTLERI AND OF CERTAIN RACES OF GUINEA-PIGS AND OF THEIR HYBRIDS  
CLASS 1 INCLUDES MEASUREMENTS 29.5-29.9 MM.

0.5 MM. CLASSES																													TOTALS	MEANS	$\sigma$
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27					
♀ C. Cutleri.....																													10	30.84	9.35
♀ Race B.....																													28	34.68	10.56
♀ F <sub>1</sub> Cutleri × Race B.....																													24	35.24	11.60
♀ F <sub>2</sub> Cutleri × Race B.....																													33	33.26	11.45
♂ C. Cutleri.....																													7	31.63	6.80
♂ Race B.....																													63	36.33	11.90
♂ F <sub>1</sub> Cutleri × Race B.....																													26	37.79	11.70
♂ F <sub>2</sub> Cutleri × Race B.....																													24	35.24	12.05
♀ F <sub>1</sub> Areq. × Race B.....																													18	38.37	9.40
♀ F <sub>2</sub> Areq. × Race B.....																													41	37.35	14.05
♂ F <sub>1</sub> Areq. × Race B.....																													27	39.40	11.95
♂ F <sub>2</sub> Areq. × Race B.....																													56	38.87	11.40

TABLE 3  
VARIATION IN FEMUR-LENGTH OF CAVIA CUTLERI AND OF CERTAIN RACES OF GUINEA-PIGS AND OF THEIR HYBRIDS  
CLASS 1 INCLUDES MEASUREMENTS 35.5-35.9 MM.

	0.5 MM. CLASSES																								TOTALS	MEANS	$\sigma$
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24			
♀ C. Cutleri.....	1	1	1	1	1	1	3	2	3	2	6	5	5	1	1										12	38.45	12.05
♀ Race B.....							3																		29	41.16	12.50
♀ F <sub>1</sub> Cutleri × Race B.....											2	2	2	4	2	4	6	1							23	42.63	10.35
♀ F <sub>2</sub> Cutleri × Race B.....	1					2	1	5	3	6	2	6	3		3	1									33	40.38	15.60
♂ C. Cutleri.....					2	2	2	2	1																7	38.77	8.20
♂ Race B.....								1		2	6	9	10	12	4	3	3	1	1						52	42.39	10.70
♂ F <sub>1</sub> Cutleri × Race B.....									1					4	2	5	3	4							19	43.57	9.80
♂ F <sub>2</sub> Cutleri × Race B.....								2	1	2	5	4	6		2	1					1				24	41.32	14.20
♀ F <sub>1</sub> Areq. × Race B.....														3	3	3	1	4	4	1	2		2		23	44.07	13.35
♀ F <sub>2</sub> Areq. × Race B.....										2	1	5	3	6	4	5	3	5	3	1	2	1			41	42.95	15.30
♂ F <sub>1</sub> Areq. × Race B.....																2	1	5		5	8	2	1	1	25	45.16	10.05
♂ F <sub>2</sub> Areq. × Race B.....										1	1	4	9	8	7	10	6	5	1				1		54	43.15	11.80

F<sub>1</sub> female hybrids between Cutleri and race B are practically as large in skull-length as race B females. Their means differ by less than half a millimeter. This harmonizes with the observations on general size as indicated by the weights given in the growth curves. The empirical range of the F<sub>1</sub> hybrids is from class 12 to class 24, just within the limits of variation of race B. The F<sub>2</sub> hybrids are considerably lower in mean skull-length than their F<sub>1</sub> parents: indeed they are strictly intermediate between pure Cutleri and race B, in complete agreement with the growth curves (fig. 2). Their mean skull-length is 54.35 mm.; the middle point between the skull-length of Cutleri and race B is just 0.5 mm. greater. Their range (if we leave out of consideration one aberrant individual) extends from the middle of the range of Cutleri to the middle of the range of race B, and would show no increase of variability over F<sub>1</sub> or race B. But the one aberrant individual makes F<sub>2</sub> more variable than F<sub>1</sub>; it is as small as the smallest Cutleri female in skull-length and also in femur length (Table 3). It was however not so small in skull-width (Table 2). Nevertheless it might pass for a very good size segregate closely resembling the Cutleri ancestor. There can be no doubt about its hybrid origin or that it was a genuine F<sub>2</sub>, not an accidental back-cross of F<sub>1</sub> with Cutleri, for it was of a color variety, cinnamon, which could not be obtained from a back-cross or from either uncrossed parental race. We shall consider its significance further.

In the second section of Table 1 are classified the skull-length measurements of Cutleri and race B males and of male hybrids between these races, both F<sub>1</sub> and F<sub>2</sub>. These show that the skull-length of males regularly exceeds that of females of like ancestry but that the relations of race to race, as regards skull-length, are the same for males as for females. Cutleri and race B do not overlap in range of skull-length in either sex. Their F<sub>1</sub> hybrids equal or exceed race B in mean skull-length, but show no greater variability. F<sub>2</sub> is intermediate in skull-length between the parental races, lacking the vigor of F<sub>1</sub> due to crossing but not a matter of heredity. There is however, among the male F<sub>2</sub> hybrids, one aberrant individual with a long skull comparable with that of the largest race B animals and Table 3 shows that one of the F<sub>2</sub> males (the same one in fact) even surpassed race B males in femur length. But in Table 2 we look in vain for an aberrant F<sub>2</sub> male of unusual skull-width. The animal in question accordingly had an unusually long but not an unusually wide skull. It also had an unusually long femur. Obviously some agency is at work which produces variation in *length* of skull and femur without greatly affecting width of skull. The aberrant F<sub>2</sub> female as well as the aberrant F<sub>2</sub> male indicate this. Whether the hypothetical

agency is genetic or purely physiological (like that which produces the large size of  $F_1$ ) is at present uncertain. If it should prove to be genetic, it may conceivably be a Mendelizing factor of greater or less stability, like those which affect the shape of fruits in tomatoes, peppers, and squashes (Gross, Emerson). But this will remain a matter of uncertainty until further evidence is forthcoming. Aside from these two individuals with skeletons of unusual *form*, everything so far indicates that the inheritance of skeletal dimensions is completely blending with physiological increase of size in  $F_1$ , this being however not a matter of heredity.

We have already anticipated the result of the Cutleri  $\times$  race B cross as regards skull-width. See Table 2. Here also the parent races scarcely overlap in range of variation. The mean of  $F_1$  slightly exceeds that of race B.  $F_2$  is intermediate between the parent races and scarcely more variable than  $F_1$ , with no very aberrant individuals.

In the lower portion of Tables 1-3 will be found the bone-measurements for the  $F_1$  and  $F_2$  generations produced by a cross between race B females and the Arequipa male, 1002, still living and so not available for bone measurements.

But bone measurements of a pair of animals of the Arequipa race are slightly less than the corresponding average measurements of the  $F_1$  animals. Hence it is probable that a considerable physiological increase of size occurs in  $F_1$  in this cross, as in the Cutleri cross, causing the production of an  $F_1$  larger than either parent race. Comparison of the growth curves of  $F_1$  and  $F_2$  (figs. 3 and 4) and of their respective bone measurements confirms this idea. The mean of  $F_2$  is in all measurements less than that of  $F_1$ , the difference amounting to one or two millimeters. This indicates that the increase of size due to crossing, seen in  $F_1$ , does not persist in  $F_2$ .

But the important question theoretically is whether there is evidence of the segregation or recombination in  $F_2$  of distinct genetic size factors. If such segregation occurs, it might be expected to show itself either (1) in increased amplitude of the variation, provided that multiple factors occur which lack dominance but segregate and recombine independently of each other, or (2) in the formation of multi-modal  $F_2$  variation curves with the production of isolated aberrant individuals, provided that the genetic factors concerned are few in number or show dominance.

As regards the first possibility, the  $F_2$  animals do show somewhat greater variability than the  $F_1$ s, though the difference as measured by the standard deviation ( $\sigma$ ) is not great. In the case of Cutleri  $\times$  race

B females, the standard deviation of  $F_2$  in skull-length (Table 1) is less than that of uncrossed race B females and is not half a millimeter greater than that of the  $F_1$ s. The difference can scarcely be regarded as significant. In skull-width the  $F_2$  females have a smaller standard deviation than the  $F_1$ s, while in femur-length alone is  $F_2$  larger than  $F_1$  and either parent race.

Among the male hybrids produced by the Cutleri  $\times$  race B cross, the evidence for increased variability in  $F_2$  is rather better. In skull-length (Table 1) and femur-length (Table 3) the standard deviation of  $F_2$  exceeds that of  $F_1$  or either uncrossed race. In skull-width the difference is not significant.

It should be noted in passing that the very low standard deviations of pure Cutleri animals do not necessarily indicate lack of variability, but are to be explained in part as due to the small numbers of animals available for measurement. For Pearson has shown that with numbers less than 25, the empirical standard deviation is as a rule too small. It will be observed in Tables 1-3 that the highest standard deviations among the pure Cutleri animals are found where the numbers studied are largest. As between the  $F_1$  and  $F_2$  animals studied, the numbers are not sufficiently different to make any allowance of this sort necessary. In the Arequipa  $\times$  race B crosses,  $F_2$  has a higher standard deviation than  $F_1$  in five out of six cases, the  $F_1$  animals being more variable only in the skull-width measurements of males (Table 2).

We may conclude that on the whole  $F_2$  shows consistently a higher variability than  $F_1$  in the crosses studied, which is in agreement with the observations made in numerous other hybridization experiments with both animals and plants. But it does not follow that the difference observed is due wholly to multiple genetic factors affecting size. For increased variability in  $F_2$  would occur if the physiological increase of size observed in  $F_1$  persisted to some extent in  $F_2$  but persisted unequally (i.e., in different degrees) among the different  $F_2$  zygotes. Now there is some reason to think that the non-genetic or excess vigor of  $F_1$  does persist slightly into  $F_2$ , for in 5 out of 6 cases in the Cutleri  $\times$  race B cross (Tables 1-3), the  $F_2$  mean is *greater* than the intermediate point between the means of the uncrossed races. But it is clear that if this non-genetic vigor is found to a greater extent in some  $F_2$  zygotes than in others, *it will increase the variability of the  $F_2$  zygotes as a group*.

As against the multiple factor hypothesis it may be urged further that an increased variability of  $F_2$  may be satisfactorily accounted for in still other ways without involving multiple factors, as for example by quantitative variation in a single factor affecting total growth energy of the zygote.

We come now to the alternative question whether evidence is forthcoming of a *few* genetic factors or of single genetic factors affecting size, showing themselves in multimodal variation or in aberrant individuals. There is in Tables 1-3 no evidence of multimodal variation. As regards aberrant individuals we have two and only two notable cases, which are found in  $F_2$  of the Cutleri  $\times$  race B cross, as already stated. These are (1) a female with very short skull and femur closely resembling pure Cutleri females in these measurements, but not in skull-width, and (2) a male with very long skull and femur, closely resembling race B animals in these respects but not in skull-width. It seems quite possible that some special factor affecting duration of growth is concerned in the production of these extreme individuals. Thus castration of cattle is known to permit abnormally prolonged growth of the skeleton *in length*. Early sexual maturity is probably correlated with an opposite change. Whether physiological factors affecting the sexual system are concerned in the production of these unusual individuals, or whether genetic agencies are concerned is at present uncertain. It is regrettable that the exceptional character of these two individuals was not recognized while they were still alive and so capable of genetic tests. Possibly further investigations now in progress may throw light on these questions.

If the foregoing reasoning is sound, we have from these crosses no evidence showing either the existence of *numerous* multiple Mendelian factors affecting size, or the existence of a *few* Mendelian factors affecting size, or the existence of a *single* Mendelian factor affecting size. We have however clear evidence of a physiological factor causing a marked increase of size in  $F_1$  and probably persisting to a small extent in  $F_2$  and so increasing slightly the variability of  $F_2$ . This factor, though its existence has long been known, has been largely neglected in those recent studies of size inheritance which seek to give a Mendelian interpretation of the phenomena observed in size crosses, and it is quite possible that this neglect has caused erroneous conclusions to be reached.

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